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SURVEY ARTICLE

Dormancy in Stochastic Population Models

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1 Introduction

Dormancy in biological populations refers to the ability of an organism to enter a reversible state of metabolic inactivity. It appears in many guises, the most obvious being plants that produce seeds. In their seed-form they can remain inactive in the ground for years, even decades, and withstand adverse conditions before finally germinating again. Resuscitating from dormancy re-introduces old genetic material into the present time population thus leading to an increase in genetic variability. Dormancy, however, is much more widespread and appears under different names and with varying mechanisms also in microbial communities as well as in cancer cells or neurological systems, leading to a variety of phenomena that are of practical relevance e.g. in medicine, and of theoretical interest e.g. in understanding the mechanisms of evolution [58].

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Modelling complex stochastic interacting systems with dormancy is a relatively recent field that started with models from population genetics [7, 52, 55], and soon sparked interest within the community of probabilists working on stochastic models of population genetics (including coalescent models), population dynamics (e.g. adaptive dynamics and branching processes), S(P)DEs (e.g. the stochastic F-KPP equation) and interacting particle systems (e.g. exclusion process). It turns out that including dormancy into mathematical (individual based) stochastic models leads to interesting and sometimes astonishing effects such as particle flows against the gradient direction [33].

As such, dormancy is also an example of how a biological motivation can drive the development of theoretical results beyond the original field and we would thus like to showcase this phenomenon and the resulting recent developments to a broader audience through this review.

We focus on the historic origin of the modelling of dormancy in population genetics as the most accessible of the models thereby giving the interested reader an understanding of the effects of dormancy and at the same time an overview of typical problems, objects and techniques used in population genetics in general. Two further examples – spatial modelling through the Fisher-KPP equation and the effect of random environment – are also presented with some detail while further developments will only be briefly outlined. In general, we omit proofs (but give references) and focus on the results and their explanations, except in the cases where the proofs are short and of explanatory value.

We start with a gentle introduction into classical stochastic population genetics models in Sect. 2.1, and then present an extension of this framework that includes dormancy in Sect. 2.2. We analyse this model to show the effect of dormancy in Sect. 2.2.4 (*fixation/extinction*). We then extend the model to include coordinated switching, i.e. when several individuals move in or out of dormancy *simultaneously* and discuss another effect of dormancy within this framework (*coming down from infinity - or not*) in Sect. 2.3. We discuss some aspects of spatial models including the stochastic F-KPP equation and branching Brownian Motion with dormancy in Sect. 3 and present a framework to study different dormancy strategies in a random environment in Sect. 4. Finally, in Sect. 5, we outline some further developments in related fields for the interested reader. The sections are largely independent of each other and can thus be read in order of most interest to the reader.

2 The Original Motivation: Dormancy in Population Genetics

Population genetics as a field of applied mathematics has a long tradition that goes back to the early 20th century and works by Fisher, Wright and Haldane. At the centre of this were models for the evolution *forward in time* of the frequency of an allele in a population subject to different evolutionary forces. Their analysis also drove general theory in stochastic analysis leading for example to Feller's one-dimensional diffusion theory and boundary classification [2]. The introduction of the opposite viewpoint *backward in time*, i.e. the study of genealogies, by Kingman in the 80s paved the way for the mathematical methods of modern statistical data analysis. The

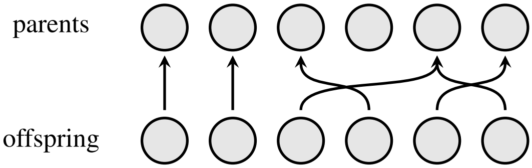


Fig. 1 Illustration of one generation in the Wright-Fisher model for $N = 6$: each individual in the offspring generation chooses independently, uniformly at random an individual from the parental generation

stochastic duality between the forward and the backward processes added a powerful tool for the analysis of the systems. The framework has been extended under numerous aspects, and the methods used range from Markov chains, coalescent theory, measure valued stochastic processes and stochastic partial differential equations (SPDEs) to statistics and data analysis.

Before we start to mathematically model dormancy, we give an introduction to the *Wright-Fisher framework*, that will provide the foundation of our modelling of dormancy in Sect. 2.2. Readers familiar with this field may want to skip this subsection.

2.1 A Classic Model from Population Genetics

Models in population genetics often start out from an *individual based model* describing the mechanism of reproduction to be studied, then takes into account the large population size and long evolutionary time-scales to obtain suitable limiting objects with distinguished characteristics. The most classic model – the Wright-Fisher model with the Wright-Fisher diffusion and the Kingman coalescent as scaling limits – is still the prevalent null-model up to today, and has been extended to incorporate many evolutionary forces such as mutation, selection, recombination, geographic space, random environments or dormancy, to name just a few. Most importantly, it should be noted that already the very basic model of reproduction is probabilistic, since the mechanisms driving reproduction and thus the genetic variability even of a large population are intrinsically stochastic. The content of this section is standard and can be found for example in [29].

The *Wright-Fisher model* describes the dynamics of a neutral, haploid population of constant size N evolving in discrete time steps (called generations) indexed by $r \in \mathbb{N}_0$. "Neutral" means that each individual has the same reproductive strength, i.e. there is no selection, no individual (or type) is fitter than the other. "Haploid" means that there is only one copy of each chromosome and thus each individual has only one parent. This assumption is not as abstract as it may seem, but rather realistic in particular if "individuals" are single genes. Likewise the assumption of constant population size N is typically sufficiently satisfied on the time-scales considered. The population of generation $r + 1$ consists of N individuals that are the children of the N individuals from the previous generation r. To model the constant population size, we may think that each child "chooses" its parent uniformly at random from the population, independently of each other, see Fig. 1. As a result, the joint distribution of the number of offspring of all individuals in generation r is symmetric multinomial, underlining the assumption of "neutrality". This mechanism is repeated independently for all generations.

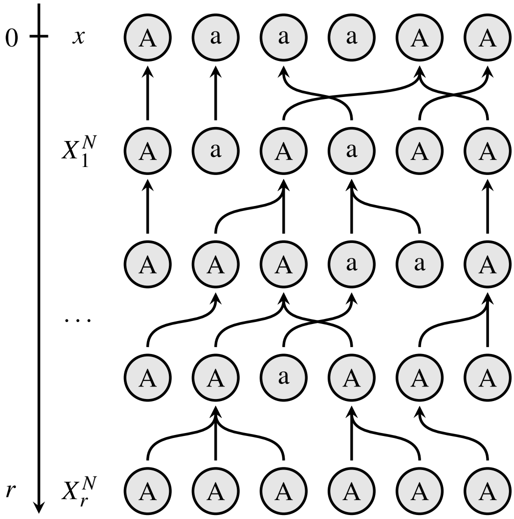


Fig. 2 Illustration of the evolution of types in the Wright-Fisher model

Based on this model, two processes can be studied to describe the evolution of the population. Historically the first one was that of going *forward in time*. We assume our individuals are one of (for simplicity only) two alleles (genetic types) which we call a and A and which are inherited by the children from their parent. The quantity of interest is then X_r^N, the proportion or frequency of individuals with type a in the population at generation r. By the above description of the model, $(X_r^N)_{r\in\mathbb{N}_0}$ is a Markov chain with state space $\{0, 1/N, \dots, 1\}$ and transition probabilities

$$\mathbb{P}\Big[X_{r+1}^N = \frac{i}{N}\,\Big|\,X_r^N = \frac{j}{N}\Big] = \binom{N}{i}\left(\frac{j}{N}\right)^i\left(1-\frac{j}{N}\right)^{N-i},$$

where $i, j \in \{0, \dots, N\}$, i.e. $N \cdot X_{r+1}^N$ is a binomial random variable with parameters N and X_r^N. The stochastic process $(X_r^N)_{r\in\mathbb{N}_0}$ is called the *frequency process of the Wright-Fisher model* and illustrated in Fig. 2. Notice that the states 0 and 1 are absorbing, i.e. if reached, the process will remain in them forever.

It is easy to calculate that

$$\mathbb{E}\Big[X_{r+1}^N\,\Big|\,X_r^N\Big] = X_r^N \quad \text{and} \quad \mathbb{V}\Big[X_{r+1}^N\,\Big|\,X_r^N\Big] = \frac{1}{N}X_r^N\big(1-X_r^N\big).$$

Hence, $(X_r^N)_{r\in\mathbb{N}_0}$ is a martingale with respect to the natural filtration, i.e. a “fair game” from the point of view of the two allelic types in the population, which again reflects the desired neutrality of the model. In particular, a straightforward application of Doob’s stopping theorem for martingales shows that the probability that type a *fixates* in the population (or equivalently, that type A becomes extinct), i.e. that the process is absorbed in 1 and not in 0, is given exactly by the initial frequency X_0^N of this type. Moreover, the term for the variance reflects that the order of the strength of the randomness in each generation is $1/N$ and hence we will have to scale time with N in order to retain the randomness in a scaling limit.

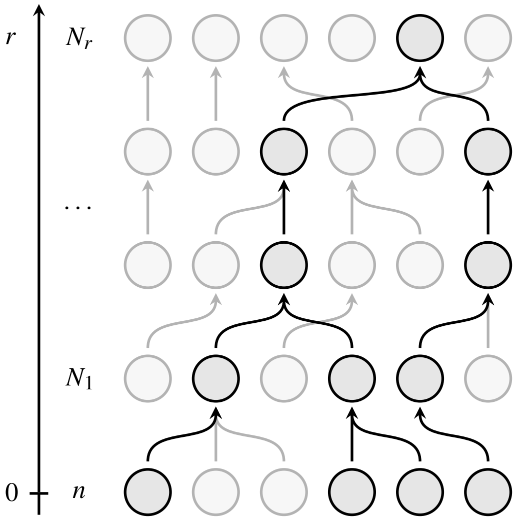


Fig. 3 Illustration of the genealogy of a sample of $n = 4$ individuals in the Wright-Fisher model. In generation r the sample finds their *most recent common ancestor*

Indeed, the central result in this field is that the time-rescaled stochastic process $(X^N_{\lfloor Nt \rfloor})_{t\geq 0}$ converges weakly as $N \to \infty$ to the solution $(X_t)_{t\geq 0}$ of the stochastic differential equation

$$\mathrm{d}X_t = \sqrt{X_t(1 - X_t)}\,\mathrm{d}B_t \tag{2.1}$$

called the *Wright-Fisher diffusion*. Here, $(B_t)_{t\geq 0}$ denotes a standard Brownian motion. It shares many properties with its discrete origin, although it is, of course a much more complex object: It is also a Markov process and a Martingale. 0 and 1 are absorbing states and the Wright-Fisher diffusion will indeed reach one of these in finite time ($\mathbb{P}$-almost surely), where the probability of being absorbed in 1 is again given by the initial frequency X_0.

On the other hand, one can describe the evolution of a population by going *backwards in time* and tracing the *genealogy* of a sample of $n < N$ individuals in the Wright-Fisher model, as described in Fig. 3. This gives a rather simple Markov chain that can only see lineages coalesce and will thus eventually end up with only one lineage. The first time this happens we speak of *the most recent common ancestor* of the sample. Note that two fixed individuals in the same generation will find their common ancestor in the previous generation with probability $1/N$. Since we assumed independence of the generations, the number of generations one needs to go back in time to find the common ancestor of two fixed individuals is geometrically distributed with success parameter $1/N$ and therefore converges to an exponential random variable with parameter 1 if we rescale time by N as we did before. The probability that three or more individuals find their common ancestor in the previous generation or that two or more pairs of individuals find their respective common ancestors is of order smaller than $1/N^2$ and hence disappears under the same time-rescaling. Hence, rescaling time to $\lfloor tN \rfloor$, we should see pairs of lineages in the genealogy coalesce at rate 1 independently of each other, with no other possible transitions.

This is indeed the case and if we only trace the *number* of ancestors of the sample, we obtain in the limit $N \to \infty$ on the time-scale $\lfloor tN \rfloor$ a continuous time Markov chain $(N_t)_{t\geq 0}$ with values in $\mathbb{N}$, initial value $N_0 = n$ the sample size, and transition rate given by

$$n \longmapsto n-1 \text{ at rate } \binom{n}{2},$$

i.e. a Markov chain that decreases by one at a rate given by the number of possible pairs of lineages. We call $(N_t)_{t\geq 0}$ the *block counting process of the Kingman coalescent*. Indeed, instead of just the number of lineages one can also consider the whole genealogy encoded as partitions of $\{1, \ldots, n\}$ where each block contains the labels of the individuals in the original sample that have merged into the current line. This is the famous *Kingman coalescent* [53], which is crucial for modern-day genome-based statistical methods.

The Wright-Fisher diffusion and the Kingman coalescent thus describe the evolution of the same population once forward and once backward in time. Their close interrelation can also be expressed mathematically: The Wright-Fisher diffusion and the block-counting process of the Kingman coalescent are *moment-duals*, i.e. for any $n \in \mathbb{N}$, $x \in [0, 1]$ and $t \geq 0$

$$\mathbb{E}_x\big[X_t^n\big] = \mathbb{E}_n\big[x^{N_t}\big], \tag{2.2}$$

where $\mathbb{E}_x$ is the expectation conditioned on the initial value $X_0 = x$, and $\mathbb{E}^n$ is the expectation given $N_0 = n$. This duality is one of the main mathematical tools in the analysis of the processes and we will illustrate its use below for the model including dormancy.

2.2 Introducing Dormancy

A first step to incorporate dormancy in a Wright-Fisher-model was taken in [52]. Here, individuals choose their ancestor not from the previous generation, but from a generation sampled at random from the past. As long as this range has a finite expectation, the resulting coalescent will still be a Kingman coalescent, but stretched, cf. [5], hence this effect is referred to as *weak seed bank effect*. It is tailored to the backwards-in-time point and thus amenable to inference methods [68, 71].

It is also possible to incorporate dormancy and develop the full framework we saw in the previous section. Since the resulting objects will differ significantly from the model without dormancy, this is referred to the *strong seed bank effect*. It was introduced in [7], where most of the content of this section is taken from.

We consider our population to now consist of two sub-populations: In addition to the N individuals forming the *active* population, there are $M \in \mathbb{N}$ *dormant* individuals, forming a *seed bank*. Again, the sizes N and M of the active and dormant populations are fixed, and the population evolves in discrete generations with each individual having only one parent. Fix now a number $c \leq \min\{N, M\}$. The dynamics of the *Wright-Fisher-model with dormancy* is given as follows:

At each time step, all N active individuals reproduce by multinomial sampling to produce N offspring. Among those offspring, c chosen uniformly at random without

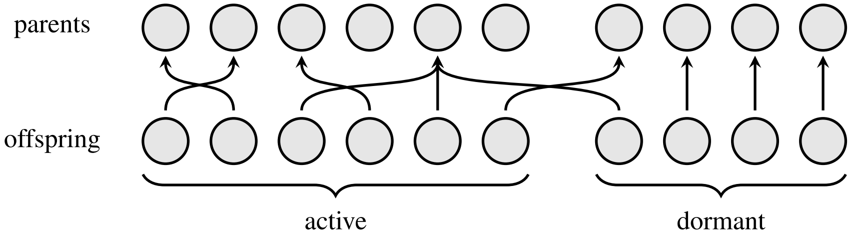


Fig. 4 Illustration of the sampling mechanism in the seed bank model for $N = 6$ active individuals, $M = 4$ dormant individuals and an exchange of $c = 1$ individual per generation. Active individuals in the parent generation reproduce by multinomial sampling, i.e. are chosen uniformly at random with replacement by $N - c$ active and c dormant offspring. Dormant parents simply copy themselves into the next generation with $M - c$ copies in the seed bank and c in the active generation

replacement become dormant. At the same time, c individuals chosen uniformly at random without replacement from the dormant population germinate, while the other $M - c$ individuals remain inactive in the seed bank. This is corresponds to saying that $N - c$ active offspring and c dormant offspring choose their parent independently uniformly *with* replacement from the *active parent* generation, while $M - c$ dormant offspring and c active offspring choose a parent *without* replacement from the *dormant parent* generation, as illustrated in Fig. 4.

The interpretation of active and dormant population in this model is thus straightforward: Only active individuals may reproduce at random, while dormant individuals simply have one copy of themselves in the next generation. Moreover, there is an exchange between active and dormant population such that both parts of the population retain constant size. As before, we can trace two processes on this structure.

2.2.1 Forward in Time Seed Bank Model

Again, each individual has a type a or A, and types are passed on to the offspring, resp. kept while the individual is dormant, see Fig. 5. We label the individuals of the active population by $i \in \{1, \dots, N\}$ and in the dormant population by $j \in \{1, \dots, M\}$. The object of interest is now the two-dimensional Markov chain $(X_r^N, Y_r^M)_{r \in \mathbb{N}_0}$ with

$$X_r^N = \frac{1}{N} \sum_{i=1}^{N} \mathbb{1}_{\{\text{ind. } i \text{ in gen. } r \text{ is of type } a\}} \quad \text{and} \quad Y_r^M = \frac{1}{M} \sum_{j=1}^{M} \mathbb{1}_{\{\text{ind. } j \text{ in gen. } r \text{ is of type } a\}}$$

counting the proportion of individuals of type a in the active, resp. in the dormant part of the population. The state space of this process is given by $\{0, 1/N, \dots, 1\} \times \{0, 1/M, \dots, 1\} \subset [0, 1]^2$. The above dynamics can clearly be formalised into transition probabilities for $(X_r^N, Y_r^M)_{r \in \mathbb{N}_0}$:

Lemma 2.1 (Proposition 2.2 in [7]) *Assume $X_0 = x$, $Y_0 = y$. Let U, V, W be independent random variables, where U is binomial with parameters $N - c$, x, V is binomial with parameters c and x and W is hypergeometric with parameters M, yM and c. Then, the distribution of (X_1, Y_1) is the same as the distribution of $\big((U + W)/N, y + (V - W)/M\big)$.*

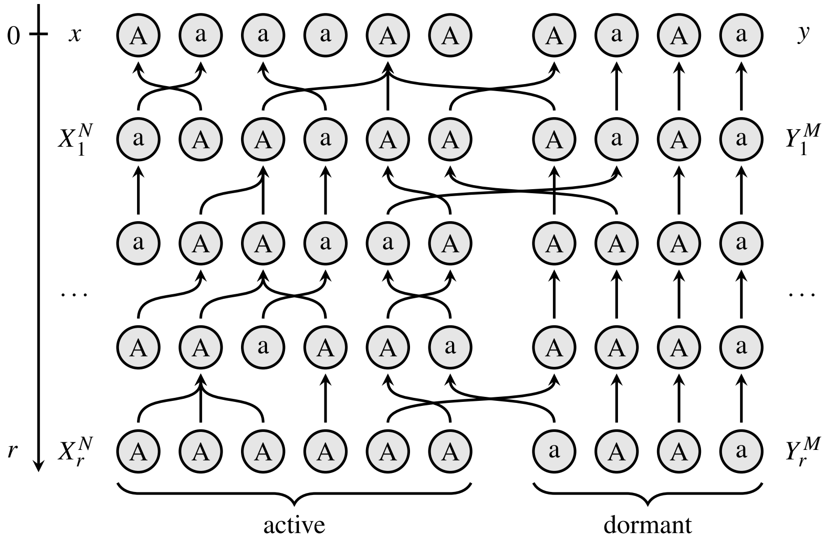


Fig. 5 Illustration of the evolution of types in the Wright-Fisher model with seed bank

Proof The proof is a straightforward from the interpretation of the random variables involved. Note that U is the number of *active offspring* with *active parents*. V on the other hand is the number of *dormant offspring* with *active parents*. And W is the number of *active offspring* with *dormant parents*. The number of *dormant offspring* with *dormant parents* is thus $yM - W$ and the claim follows. □

If we assume that c does not depend on the overall population size, i.e. that the fraction of active individuals going dormant is always c/N, and that the active and dormant population sizes are of the same order, using generator calculations based on Ethier and Kurtz [30] we again obtain a limit when scaling time with the size of the active population N:

Theorem 2.1 (Corollary 2.5 in [7]) *Assume that there exists* $K > 0$ *such that* $M = N/K$. *If* $X_0^N \to x \in [0, 1]$ *and* $Y_0^N \to y \in [0, 1]$ *as* $N \to \infty$, $\mathbb{P}$-*a.s., we have that* $(X_{\lfloor Nt \rfloor}^N, Y_{\lfloor Nt \rfloor}^M)_{t \geq 0}$ *converges weakly in* $D_{[0,\infty)}([0, 1]^2)$ *to the solution* $(X_t, Y_t)_{t \geq 0}$ *of*

$$\begin{aligned} \mathrm{d}X_t &= c(Y_t - X_t)\,\mathrm{d}t + \sqrt{X_t(1 - X_t)}\,\mathrm{d}B_t \\ \mathrm{d}Y_t &= cK(X_t - Y_t)\,\mathrm{d}t. \end{aligned} \tag{2.3}$$

Here, $(B_t)_{t \geq 0}$ *is a standard one-dimensional Brownian motion, and* $D_{[0,\infty)}([0, 1]^2)$ *denotes the space of càdlàg functions from* $[0, \infty)$ *to* $[0, 1]^2$ *endowed with the Skorokhod topology.*

The stochastic process $(X_t, Y_t)_{t \geq 0}$ defined as the unique strong solution to the stochastic differential equation (2.3) is called the *seed bank diffusion* and can also be

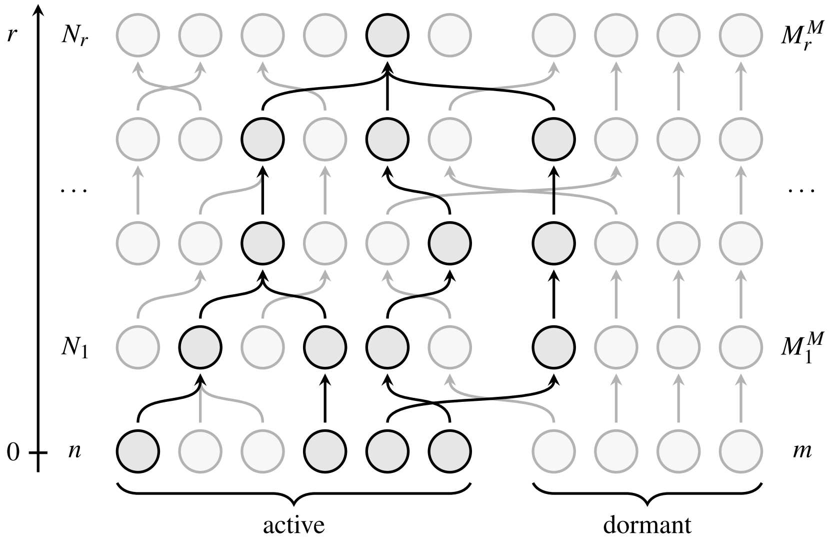


Fig. 6 Illustration of the genealogy of a sample of $(n, m) = (4, 0)$ individuals in the Wright-Fisher model with seed bank. The ancestral lines can coalesce in the active population or migrate between the active and the dormant population. In the rth generation the sample finds their *most recent common ancestor*

characterised by the generator of its Markov-semigroup

$$(Af)(x, y) = c(y - x)\partial_x f(x, y) + cK(x - y)\partial_y f(x, y) + \frac{1}{2}x(1 - x)\partial_{xx} f(x, y) \tag{2.4}$$

for suitably smooth functions $f : [0, 1]^2 \to \mathbb{R}$ (cf. Prop. 2.4 and accompanying remarks). It is a two-dimensional diffusion process, where only the first component X_t describing the evolution of the frequency of the a allele in the active population is subject to a noise-term describing reproduction given by the Wright-Fisher diffusion. In addition, there is an exchange between the two components in the form of a migration term. Clearly, $(0, 0)$ and $(1, 1)$ are again absorbing states, but the seed bank diffusion differs in the absorption behaviour from the Wright-Fisher diffusion as we will discuss below in Sect. 2.2.4.

2.2.2 Backward in Time Seed Bank Model

We can again change to the genealogical viewpoint, and consider the line counting process of the genealogy. Starting with a sample of $n < N$ active and $m < M$ dormant individuals, we trace a two-dimensional process counting the number of ancestors of the initial sample that are active and dormant respectively, see Fig. 6. If we assume, as in Theorem 2.1, that the active and dormant population sizes are of the same order (given by a factor K) and that c is fixed, i.e. the number of individuals switching into or out of dormancy is of order c/N, then scaling time to $\lfloor tN \rfloor$ as before, in the limit as $N \to \infty$, we obtain the *block-counting process of the seed bank coalescent*, a Markov process $(N_t, M_t)_{t\geq 0}$ with transition rates

$$(n,m) \longmapsto \begin{cases} (n-1, m+1) & \text{at rate } cn, \\ (n+1, m-1) & \text{at rate } cKm, \\ (n-1, m) & \text{at rate } \binom{n}{2}, \end{cases} \tag{2.5}$$

see [7, Corollary 3.5] for the corresponding result for the full seed bank coalescent. The possible transitions have clear interpretations: the first is a switch from active to dormant by one of the lineages (i.e. backward in time); the second is a switch from dormant to active; and the third is the coalescence of two lines in the active population (corresponding to a reproduction in the forward picture). Note that dormant lineages cannot coalesce, neither with an active nor another dormant line, as is expected since dormant individuals cannot reproduce. This lack of coalescence in the dormant population has far-reaching consequences for the characteristics of the genealogy as we will discuss in Sect. 2.3.2 below.

2.2.3 Duality

As mentioned, we obtain the full Wright-Fisher framework, including a duality relation between the forward and backward in time processes, which generalises (2.2). Again, denoting by $\mathbb{E}_{x,y}$ the expectation conditioned on the starting point $(X_0, Y_0) = (x, y)$ of the seed bank diffusion, and by $\mathbb{E}^{n,m}$ the expectation conditioned on the starting point $(N_0, M_0) = (n, m)$,

Theorem 2.2 (Thmeorem 2.8 in [7]) *For every* $(x, y) \in [0, 1]^2$, *every* $n, m \in \mathbb{N}_0$, *and every* $t \geq 0$

$$\mathbb{E}_{x,y}\big[X_t^n Y_t^m\big] = \mathbb{E}^{n,m}\big[x^{N_t} y^{M_t}\big]. \tag{2.6}$$

Because the proof illustrates a standard approach in this field, we have decided to include its key step that relies on the generator representation of the two processes.

Proof Recall the definition of the generator of the seed bank diffusion in (2.4) and note that the rates given in (2.5) translate to the generator B of the block-counting process of the seed bank coalescent acting on $g\colon \mathbb{N}_0^2 \to \mathbb{R}$ as

$$\begin{aligned}(Bg)(n,m) = cn\big(g(n-1,m+1) - g(n,m)\big) + \binom{n}{2}\big(g(n-1,m) - g(n,m)\big) \\ + cKm\big(g(n+1,m-1) - g(n,m)\big).\end{aligned}$$

For any $(x, y) \in [0, 1]^2$ and $(n, m) \in \mathbb{N}_0^2$ set $f^{n,m}(x, y) := g_{x,y}(n, m) := x^n y^m$. Then we see that

$$\begin{aligned}&(Af^{n,m})(x,y) \\ &\quad = c(y-x)nx^{n-1}y^m + \frac{1}{2}x(1-x)n(n-1)x^{n-2}y^m + cK(x-y)x^n m y^{m-1}\end{aligned}$$

$$= cn\big(x^{n-1}y^{m+1} - x^n y^m\big) + \binom{n}{2}\big(x^{n-1}y^m - x^n y^m\big) + cKm\big(x^{n+1}y^{m-1} - x^n y^m\big)$$

$$= (Bg_{x,y})(n,m).$$

Since $(N_t, M_t)_{t\geq 0}$ is Feller, the remainder of the proof follows from [48, Proposition 1.2]. ☐

Note that using the notation from the proof, the duality in (2.6) can be written as $\mathbb{E}_{x,y}\big[h(X_t, Y_t, n, m)\big] = \mathbb{E}^{n,m}\big[h(x, y, N_t, M_t)\big]$ and the proof in essence requires that the generators fulfil a similar duality relation. Since $h(x, y, n, m) = x^n y^m$ are the moments, this duality is called moment-duality. This is a powerful tool as it allows one in particular to study the complex diffusion through the much simpler Markov chain. This is possible, because the quantities in (2.6) uniquely determine the distributions in question: the left-hand-side characterises the distribution of (X_t, Y_t) through the uniqueness of the Hausdorff-moment problem on $[0, 1]^2$; the right-hand side is indeed the probability generating function of (N_t, M_t). We give an example of an application in the following section.

2.2.4 Fixation and Extinction Under Dormancy

As observed above, $(0, 0)$ and $(1, 1)$ are absorbing states for the seed bank diffusion $(X_t, Y_t)_{t\geq 0}$ introduced in Sect. 2.2.1 in (2.3). They are also the only absorbing states, since absence of drift requires $x = y$, and for the fluctuations to disappear, it is necessary to have $x \in \{0, 1\}$. The moment-duality from Theorem 2.2 will allow us to show convergence and calculate the fixation probabilities for the seed bank diffusion. The first step is to conclude that the limiting moments of the diffusion do not depend in the exponents of the moments.

Lemma 2.2 (Proposition 2.9 in [7]) *All mixed moments of* $(X_t, Y_t)_{t\geq 0}$ *converge to the* same *finite limit depending only on* x, y *and* K. *More precisely, for each fixed* $n, m \in \mathbb{N}_0$, *we have*

$$\lim_{t\to\infty} \mathbb{E}_{x,y}\big[X_t^n Y_t^m\big] = \frac{y + xK}{1 + K}. \tag{2.7}$$

Proof Let $(N_t, M_t)_{t\geq 0}$ be the line counting process started in $(n, m) \in \mathbb{N}_0 \times \mathbb{N}_0$. Define a stopping time

$$T := \inf\big\{t > 0 : N_t + M_t = 1\big\}.$$

By duality (Theorem 2.2), we get

$$\begin{aligned}\lim_{t\to\infty} \mathbb{E}_{x,y}\big[X_t^n Y_t^m\big] &= \lim_{n\to\infty} \mathbb{E}^{n,m}\big[x^{N_t} y^{M_t}\big] \\ &= \lim_{t\to\infty} \mathbb{E}^{n,m}\big[x^{N_t} y^{M_t} \mid T \leq t\big]\,\mathbb{P}^{n,m}\big[T \leq t\big] \\ &\quad + \lim_{t\to\infty} \mathbb{E}^{n,m}\big[x^{N_t} y^{M_t} \mid T > t\big]\mathbb{P}^{n,m}\big[T > t\big].\end{aligned}$$

The second summand on the right hand side disappears, since $\mathbb{E}^{n,m}\big[x^{N_t}y^{M_t} \mid T > t\big] \le 1$, and $\lim_{t\to\infty}\mathbb{P}^{n,m}\big[T > t\big] = 0$ because T has finite expectation if started at finite (n, m) ($N_t + M_t$ decreases after exponential waiting times). For $T \le t$ there is only one line left at time t, which switches between active and dormant, giving

$$\begin{aligned}
&\lim_{t\to\infty}\mathbb{E}^{n,m}\big[x^{N_t}y^{M_t} \mid T \le t\big]\mathbb{P}^{n,m}\big[T \le t\big]\\
&\quad= \lim_{t\to\infty}\Big(x\mathbb{P}^{n,m}\big[(N_t, M_t) = (1,0), T \le t\big] + y\mathbb{P}^{n,m}\big[(N_t, M_t) = (0,1), T \le t\big]\Big)\\
&\quad= \lim_{t\to\infty}\Big(x\mathbb{P}^{n,m}\big[(N_t, M_t) = (1,0)\big] + y\mathbb{P}^{n,m}\big[(N_t, M_t) = (0,1)\big]\Big)\\
&\quad= \frac{xK}{1+K} + \frac{y}{1+K},
\end{aligned}$$

where the last equality holds by convergence to the invariant distribution of a single particle, jumping between the two states 'plant' and 'seed' at rate c resp. cK, which is given by $(K/(1 + K), 1/(1 + K))$ and independent of the choice of n, m. □

Since the moments characterise a distribution by the Hausdorff-moment problem, this observation is indeed sufficient to obtain the law of the limit of the seed bank diffusion for $t \to \infty$:

Corollary 2.1 (Corollary 2.10 in [7]) *Given* c, K, *for any initial value* $(x, y) \in [0,1]^2$ *the diffusion* $(X_t, Y_t)_{t\ge0}$ *converges* $\mathbb{P}_{x,y}$*-almost surely as* $t \to \infty$ *to a two-dimensional random variable* (X_∞, Y_∞), *whose distribution is given by*

$$\mathcal{L}_{(x,y)}\big(X_\infty, Y_\infty\big) = \frac{y + xK}{1+K}\delta_{(1,1)} + \frac{1 - y + (1-x)K}{1+K}\delta_{(0,0)}. \tag{2.8}$$

Convergence in distribution follows from Proposition 2.2 together with the Portmanteau (e.g. [30, Theorem 3.3.1]) and Stone-Weierstraß Theorem, since it is easy to see that the distribution given in (2.8) is the only one for which all moments are equal to (2.7) by the uniqueness of the Hausdorff-moment-problem on $[0, 1]^2$, cf. [43]. Almost sure convergence follows with the observation that $(KX_t + Y_t)_{t\ge0}$ is a martingale, see [69, Corollary 2.27] for details.

Remark 2.3 (How dormancy contributes to preserve genetic diversity.) We have shown that the seed bank diffusion, like the Wright-Fisher diffusion from Sect. 2.1, will in the limit be absorbed in the boundary points ((0, 0) and (1, 1), and 0 and 1, respectively). The probability of fixation of allele a is given by $(y + xK)/(1 + K)$ which is just its initial frequency in the total population, preserving the neutrality of the model.

Absorption in the boundary corresponds to almost sure extinction of one of the types (and thus fixation of the other), i.e. a loss of genetic diversity in the population. With dormancy, however, this loss is far less severe. In contrast to the Wright-Fisher diffusion, the seed bank diffusion will not get absorbed in these boundary points *in finite time*. Indeed, it is precisely the dormant population, that will never actually touch the boundary. This can easily be seen from the representation in (2.3): For $Y_0 \in (0, 1)$, we can sandwich the component $(Y_t)_{t\ge 0}$ describing the frequency of the allele a in the dormant population between the solutions to two deterministic ODEs by removing the effect of X_t. Consider $\mathrm{d}\underline{y}_t = -cK\underline{y}_t\mathrm{d}t$ which has maximal drift towards 0 and $d\overline{y}_t = cK(1-\overline{y}_t)\mathrm{d}t$ which has maximal drift towards 1. Then

$$\forall t \ge 0: \quad 0 < \exp(-cKt) = \underline{y}_t \le Y_t \le \overline{y}_t = 1 - \exp(-cKt) < 1$$

meaning that the boundary is indeed not reached for any $t \ge 0$.

This is also reflected the dual phenomenon about the block-counting process of the seed bank coalescent discussed below in Sect. 2.3.2.

2.3 Spontaneous vs. Simultaneous Switching

In the previous model there was a lot of independence in the behaviour of the individuals with respect to the decision of switching in and out of dormancy, as can best be seen in the behaviour of the (block-counting process of the) seed bank coalescent, where lineages decide independently to go dormant at rate cK or to awaken at rate c. However, it is quite natural to observe *coordinated* or *simultaneous behaviour*, where a large fraction of the population will go dormant or awaken at the same time, for example in response to an external force such as a forest fire or treatment with antibiotics. Of course, many other switching mechanisms are possible and we discuss some more in Sect. 4, but we begin with the introduction of *simultaneous switching* here, as was done in [10].

2.3.1 Seed Bank Model with Simultaneous Switches

In the *large switching events* that we model, a macroscopic fraction of the population may switch at once from active to dormant or vice versa. In order for these large events still to lead to a sensible limit in the same scaling as before, since they are large, they have to be rare.

In order to model these events, we extend the set-up from Sect. 2.2, i.e. we start with the individual-based model. We consider again a fixed population size of N active and M dormant individuals. We have again a parameter c describing the independent migration between the active and dormant population. In addition, we need probability measures on $[0, 1]$ μ_N and ν_N. In each transition from discrete generation r to $r+1$ exactly one of the following type of events can occur:

(S) A reproductive event with a small scale switch as in Sect. 2.2:
$N-c$ active individuals are created by multinomial sampling from active parents, while c have dormant parents and $M-c$ dormant individuals stay in the seed bank, which is filled with c individuals with active parents, see Fig. 4.

(L1) A large scale switch from dormant to active: First, a random number $z \in [0, 1]$ is sampled according to μ_N. Then, independently, $\lfloor zN \rfloor$ out of the N active individuals are replaced by copies of zN uniformly chosen dormant individuals. The remaining $N - \lfloor zN \rfloor$ active individuals stay as they are. The dormant part remains as it is, see Fig. 7.

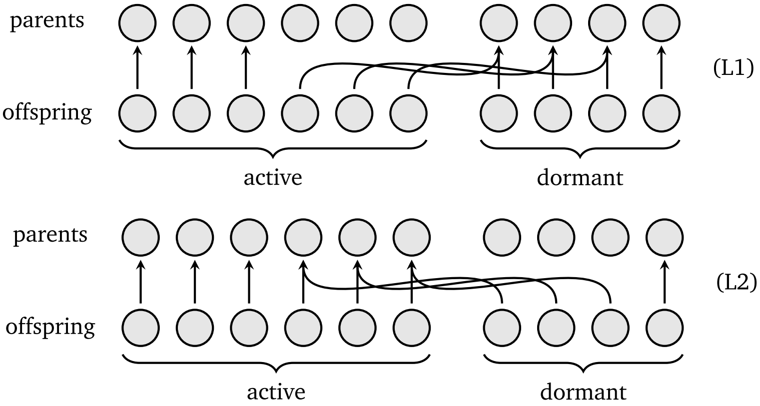


Fig. 7 Illustration of the simultaneous sampling mechanism (L1) and (L2) in the seed bank model for $N = 6$ active individuals, $M = 4$ dormant individuals and $z = 1/2$, $w = 3/4$

(L2) A large scale switch from active to dormant: First, a random number $w \in [0, 1]$ is sampled from ν_N. Then, independently, $\lfloor wM \rfloor$ out of the M dormant individuals are replaced by copies of $\lfloor wM \rfloor$ uniformly chosen active individuals. The remaining dormant individuals stay as they are. The active part of the population remains as it is, see Fig. 7.

The mechanism to decide which event occurs in each generation is simple: The a large switch from dormant to active (L1) happens with some probability $r_N \in (0, 1)$, a large switch from active to dormant (L2) with probability $s_N \in (0, 1)$, and a small scale event with probability $1 - r_N - s_N$ and this decision is taken independently for each generation. See [10] for a slightly different model and more details also on the following results.

With a careful choice of parameters one can now repeat the same set-up from Sects. 2.1 and 2.2. In particular, we obtain scaling limits forwards and backwards in time with the following assumptions: As before, we assume c not depending on N and $N = KM$ for some $K > 0$. In addition, we assume that r_N and s_N converge to 0 in such a manner that $r_N \mu_N$ weakly converges as $N \to \infty$ to some measure μ on $[0, 1]$, and $s_N \nu_N$ to a measure ν as $N \to \infty$, which both satisfy the integrability condition

$$\int_{[0,1]} z\mu(\mathrm{d}z) < \infty, \text{ resp. } \int_{[0,1]} w\nu(\mathrm{d}w) < \infty.$$

The scaling limit forward in time is then given as in [10, Sect. 1.4]:

Theorem 2.4 *Under the above assumptions, if* $X_0^N \to x \in (0, 1)$ *and* $Y_0^N \to y \in (0, 1)$ $\mathbb{P}$*-a.s. as* $N \to \infty$, *we have that* $(X^N_{\lfloor Nt \rfloor}, Y^M_{\lfloor Nt \rfloor})_{t \geq 0}$ *converges weakly in*

$D_{[0,\infty)}([0,1]^2)$ *to the solution* $(X_t, Y_t)_{t\geq 0}$ *of*

$$\begin{aligned} \mathrm{d}X_t &= c(Y_t - X_t)\,\mathrm{d}t \;+ \int_{[0,1]} z(Y_{t-} - X_{t-})\,\mathcal{N}^\mu(\mathrm{d}t, \mathrm{d}z) + \sqrt{X_t(1-X_t)}\,\mathrm{d}B_t \\ \mathrm{d}Y_t &= cK(X_t - Y_t)\,\mathrm{d}t + \int_{[0,1]} w(X_{t-} - Y_{t-})\,\mathcal{N}^\nu(\mathrm{d}t, \mathrm{d}w). \end{aligned} \tag{2.9}$$

Here, $(B_t)_{t\geq 0}$ *is a standard one-dimensional Brownian motion*, $\mathcal{N}^\mu$ *a Poisson process with intensity measure* $\lambda(\mathrm{d}t)\otimes\mu(\mathrm{d}z)$, $\mathcal{N}^\nu$ *a Poisson process with intensity measure* $\lambda(\mathrm{d}t)\otimes\nu(\mathrm{d}z)$ (*all independent of one another,* λ *is the Lebesgue measure on* $\mathbb{R}_+$), *and* $D_{[0,\infty)}([0,1]^2)$ *denotes the space of càdlàg functions from* $[0,\infty)$ *to* $[0,1]^2$ *endowed with the Skorokhod topology. The integrals in* (2.9) *are taken with respect to* $\mathrm{d}z$ *resp.* $\mathrm{d}w$.

In addition to the migration terms and the Wright-Fisher reproduction from Theorem 2.1 we now also see large scale migration events in either direction, which are given by the jump parts driven by Poisson processes. The conditions on the measures μ and ν ensure that the large jumps arrive one by one in a Poissonian way.

As before, one can consider the genealogy, and show that the limiting line counting process is given as a Markov chain on $\mathbb{N}_0^2$ with transition rates

$$(n,m) \longmapsto \begin{cases} (n-k, m+k) & \text{at rate } \binom{n}{k}\Big(c\mathbb{1}_{\{k=1\}} + \int_{[0,1]} z^k(1-z)^{n-k}\,\mu(\mathrm{d}z)\Big), \\ (n+l, m-l) & \text{at rate } \binom{n}{l}\Big(cK\mathbb{1}_{\{l=1\}} + \int_{[0,1]} w^l(1-w)^{m-l}\,\nu(\mathrm{d}w)\Big), \\ (n-1, m) & \text{at rate } \binom{n}{2}, n\geq 2, \end{cases} \tag{2.10}$$

where in the first case k is running from 1 to n, and in the second line l is running from 1 to m, with $n, m \geq 1$. Assuming again $\int_{[0,1]} z\,\mu(\mathrm{d}z) < \infty$ and analogously for ν, this process is well defined. Very similarly to Theorem 2.2 one can prove moment duality, see Sects. 1.5 in [10].

2.3.2 Coming down from Infinity

An important property of coalescents is the notion of whether they *come down from infinity* or not. Coalescents such as we have introduced here are defined for any arbitrary number of initial sample size n (respectively (n,m) in two dimensions). They satisfy a consistency property in this n an thus, using Kolmogorov's extension theorem, one can easily let them start with countably infinitely many individuals. The question is whether in this case, there will still be infinitely many individuals after a finite positive time, or if the coalesce-mechanism has decreased it to a finite number. The notion of *coming down from infinity* was introduced my Pitmann [62] and Schweinsberg [63] for exchangeable coalescents. We change their definition to say that the block-counting process $(N_t)_{t\geq 0}$ of a coalescent *comes down from infinity instantaneously*, if $\mathbb{P}\big[N_t < \infty \mid N_0 = \infty\big] = 1$ for all $t \geq 0$, that *it stays infinite forever*, if $\mathbb{P}\big[N_t < \infty \mid N_0 = \infty\big] = 0$ for all $t \geq 0$, and that it *comes down from infinity after a positive time*, otherwise. In [63] a criterion is given, showing in particular, that the block-counting process of the Kingman coalescent from Sect. 2.1 does come down from infinity.

It turns out, though, that dormancy drastically changes that behaviour:

Theorem 2.5 (Thmeorem 4.1 in [7]) *The block-counting process* $(N_t, M_t)_{t\geq 0}$ *of the seed bank coalescent* does not come down from infinity. *More precisely,*

$$\forall t \geq 0 \quad \mathbb{P}\big[M_t = \infty \mid N_0 + M_0 = \infty\big] = 1.$$

Heuristically, the explanation is as follows: The quadratic rate of the Kingman mechanism will bring down from infinity any infinite active population. However, simultaneously, the independent switching into dormancy also means that infinitely many individuals make it into the seed bank instantaneously. Since the seed bank can only be emptied at a linear rate by individuals independently waking up, although infinitely many may leave, there will always be an infinite reservoir in the seed bank. As mentioned in Sect. 2.2.4, this is tied through duality to the observation that the seed bank diffusion does not reach the absorbing point in finite time and thus to the idea that dormancy helps preserve genetic diversity.

The behaviour becomes even more interesting in the case where we add the simultaneous switching. Here we can observe all three possible regimens depending on the choices of parameters and where the infinitely many initial particles are places. In particular, we see a non-trivial example of the possibility to come down from infinity after a random time only.

In order to formulate the theorem, we need Λ to be a measure on [0, 1] satisfying

$$\Lambda[A] = \int_A z\,\mu(\mathrm{d}z)$$

for any Borel subset A of [0, 1]. By the integrability assumption on μ we made before, Λ is a finite measure, and we can normalise it to a probability measure by setting $\tilde{\Lambda} := \big[\Lambda[0, 1]\big]^{-1}\Lambda$.

Theorem 2.6 (Theorem 2.7 in [10]) *Consider the block-counting process* $(N_t, M_t)_{t\geq 0}$ *of the seed bank coalescent with simultaneous switching under the assumptions of Theorem 2.4. Let* Y *be a random variable with distribution* $\tilde{\Lambda}$.

(a) *If* $\nu[\{1\}] = 0$, *then the block-counting process started in* $(N_0, M_0) = (n, \infty)$, $n \in \mathbb{N}_0 \cup \{\infty\}$ *will stay infinite for all times.*
(b) *If the block-counting process is started in* $(\infty, m), m \in \mathbb{N}_0$, *then the process comes down from infinity instantaneously if* $\mathbb{E}\big[-\log(Y)\big] < \infty$ *and* $c = 0$. *If* $\mathbb{E}\big[-\log(Y)\big] = \infty$ *or* $c > 0$, *it stays infinite for all times.*
(c) *If* $\nu[\{1\}] > 0$, $c = 0$ *and* $\mathbb{E}\big[-\log(Y)\big] < \infty$, *then the block-counting process started from* $(n, \infty), n \in \mathbb{N}_0 \cup \{\infty\}$ *comes down from infinity after a finite time, but not instantaneously.*

Note the asymmetry in the conditions on μ, the measure governing the movement from active to dormant, and ν, the measure governing the movement from dormant to active. Heuristically, the result can again easily be explained. In (a), the infinite seed bank cannot be emptied by the spontaneous mechanism (by Theorem 2.5). The mechanism of simultaneous switching will always move a positive fraction of the population and thus an infinite number, but the remainder will always be infinite, too, since we exclude the case where the fraction is 1. For (b), note that we already know that the independent mechanism of migration from active to dormant is fast enough to save infinitely many individuals into the seed bank before the Kingman mechanism brings the numbers down from infinity, as seen in Theorem 2.5. The condition on $\mathbb{E}\big[-\log(Y)\big]$ tells us what family of measures governing the simultaneous switching mechanism are also sufficiently fast to save infinitely many individuals. Interestingly, the result states that measure favouring smaller fractions are better at competing against the Kingman mechanism, because although the others can move larger fractions of he population, the events occur too rarely. In the case (c) where we allow the measure governing the simultaneous switching from dormant to active to have an atom in 1, we will see that instantaneously infinitely many active individuals are saved into the seed bank, but this is emptied completely at once when the measure finally chooses the atom one.

The proof of this result requires some amount of technicalities, in particular various couplings and approximations by truncated processes, and we refer to [10] for details. The quantity $\mathbb{E}\big[-\log(Y)\big]$, which may look slightly mysterious at first sight, appears due to an analysis of the probabilities that at a given number of active individuals the next transition is a (possibly large) switch to dormancy before the next coalescence. The method used in this analysis is based on an approach by Griffiths, [41].

3 Dormancy and Diffusion: The F-KPP Equation with Dormancy

A currently very active area of research, motivated both from ecology and mathematics, is the analysis of the interplay of dormancy and (spatial) migration. While the latter describes *dispersal in space*, dormancy can be thought of as *dispersal in time*. Interesting trade-offs appear when both act on comparable scales, as we will indicate in this section. We will encounter a spatial extension of the classical duality in 2.2, where this time the forward-in time population model is given by the *F-KPP equation with dormancy* – and therefore deterministic. Due to the complexities of the subject, we will only state the results and some of the basic arguments, and refer to the literature for the (often long and intricate) proofs.

The F-KPP model, introduced independently by Fisher [31] and Kolmogorov, Petrovski and Piscounov [54], is known as a classical reaction-diffusion equation. However, Fishers original motivation was to describe the spread of a *beneficial allele* in a *spatial population* (in dimension 1, inhabiting e.g. a shoreline), so that this model ties in neatly with the population genetics considerations from the previous sections. It is given as the following initial value problem consisting of the partial differential equation

$$\partial_t p(t,x) = \frac{\Delta}{2} p(t,x) + p(t,x)(1 - p(t,x)), \tag{3.1}$$

in combination with an suitable initial condition $p(0,x) = p_0(x) \in \mathcal{B}(\mathbb{R}, [0,1])$ (i.e. a bounded measurable function from $\mathbb{R}$ to $[0,1]$). Here, we interpret a value of the solution $p(t,x) \in [0,1]$ as the proportion of the beneficial allele present in the population at time $t \geq 0$ in location x, thus generalising the frequency process of Sect. 2.2 to a *spatial* setup. Its dynamics is governed by the Laplacian, which models the spatial movement of individuals, and the reaction term $p(t,x)(1 - p(t,y)$, which models directional selection in the form of a fitness advantage of the beneficial allele (see e.g. [29] for the corresponding theory and motivation of directional selection).

The above system (3.1) has been studied extensively for a long time, both from an analytic as well as from a probabilistic angle. For example, it is well-known that for each $\lambda \geq \lambda^* := \sqrt{2}$, the system admits monotone travelling-wave solutions of speed λ, taking the form

$$p(t,x) = w(x - \lambda t),$$

where w is decreasing and satisfies

$$\lim_{x \to -\infty} w(x) = 1 \quad \text{and} \quad \lim_{x \to \infty} w(x) = 0. \tag{3.2}$$

The *critical wave speed* $\lambda^* = \sqrt{2}$ emerges if one starts the system from a Heaviside initial condition $p_0(x) = \mathbb{1}_{(-\infty,0)}$. For these (and many further) results we refer to the seminal works [19, 20, 57, 60].

In the context of probability theory, it is common to consider the proportion of the *deleterious allele* by defining

$$u(t,x) := 1 - p(t,x)$$

now solving the *equivalent* Cauchy problem

$$\partial_t u(t,x) = \frac{\Delta}{2} u(t,x) - u(t,x)(1 - u(t,x)), \tag{3.3}$$

with $u(0,x) = u_0 = 1 - p_0$. The reason for this transformation is that the new system now has an interesting *dual process*, namely *branching Brownian motion* (BBM), which is not available for the original system.

Branching Brownian motion can be viewed as a system of particles that move independently according to a Brownian motion, and that branch (split into two) at certain rates. The duality is a direct spatial extension of our moment duality from Theorem 2.2 and has already appeared in [67] and [45–47], and subsequently popularised and heavily used in [60] and [19]. For more general accounts on spatial dualities, see e.g. [66] and [1]. We will discuss this duality, and BBM, in a more general set-up below.

In much the same way as for the Wright-Fisher diffusion, the F-KPP equation can now be extended to accommodate *dormancy*. This has recently been carried out in

[13] and [14], where the proofs of the results stated here can be found. The approach is similar to the one taken in Sect. 2.2 - individuals may switch into and out of dormancy at constant rates. Note however that there are now at least two basic ways in which dormancy, dispersal and selection can interact in the spatial set-up.

The perhaps most natural model assumes that individuals in the dormant state neither experience selective pressure nor move in space (think of plant seeds or microbial cysts remaining static in soil). This leads to the following equation, which we call the seed bank F-KPP equation [14, Def. 1.1]:

Definition 3.1 (F-KPP equation with dormancy, I: Seed bank model) The initial value problem associated with the *F-KPP equation with dormancy, variant I*, is given by the coupled system

$$\begin{aligned} \partial_t u(t,x) &= \frac{\Delta}{2} u(t,x) + c\big(v(t,x) - u(t,x)\big) + su(t,x)\big(u(t,x) - 1\big), \\ \partial_t v(t,x) &= c'\big(u(t,x) - v(t,x)\big), \end{aligned} \tag{3.4}$$

with initial conditions $u_0, v_0 \in \mathcal{B}(\mathbb{R}, [0, 1])$, switching parameters $c, c' \geq 0$, and selection strength $s \geq 0$.

However, it is quite often the dormant form that moves – think of seeds transported by a current in oceans (as already investigated extensively by Darwin in his *Origin of Species*) – or spores being dispersed by the wind. This leads to the second model, where the active individuals still experience selective pressure, but it is the dormant forms that move [14, Def. 1.2]:

Definition 3.2 (F-KPP equation with dormancy, II: The spore model) The initial value problem associated with the *F-KPP equation with dormancy, variant II*, is given by the coupled system

$$\begin{aligned} \partial_t \tilde{u}(t,x) &= \tilde{c}\big(\tilde{v}(t,x) - \tilde{u}(t,x)\big) + s\tilde{u}(t,x)\big(\tilde{u}(t,x) - 1\big), \\ \partial_t \tilde{v}(t,x) &= \frac{\Delta}{2} \tilde{v}(t,x) + \tilde{c}'\big(\tilde{u}(t,x) - \tilde{v}(t,x)\big), \end{aligned} \tag{3.5}$$

with initial conditions $\tilde{u}_0, \tilde{v}_0 \in \mathcal{B}(\mathbb{R}, [0, 1])$ switching parameters $\tilde{c}$, $\tilde{c}'$, and selection strength $s \geq 0$.

Note that the Laplacian in this model, which we also call the *spore model*, has thus moved from the first to the second component.

Both of the above systems have interesting duals, which we subsume as *on/off branching Brownian motions (on/off BBM)*. However, the precise dynamics differ for the two variants. We begin with the dual for variant I and give an informal description to keep notation simple. Further details can again be found in [14].

On/off branching Brownian motion (variant I) is a branching Markov process, in which we label each particle by $\boldsymbol{a}$ for active or $\boldsymbol{d}$ for dormant, so that it will take values in $\Gamma := \bigcup_{k\in\mathbb{N}_0} \big(\mathbb{R} \times \{\boldsymbol{a}, \boldsymbol{d}\}\big)^k$.

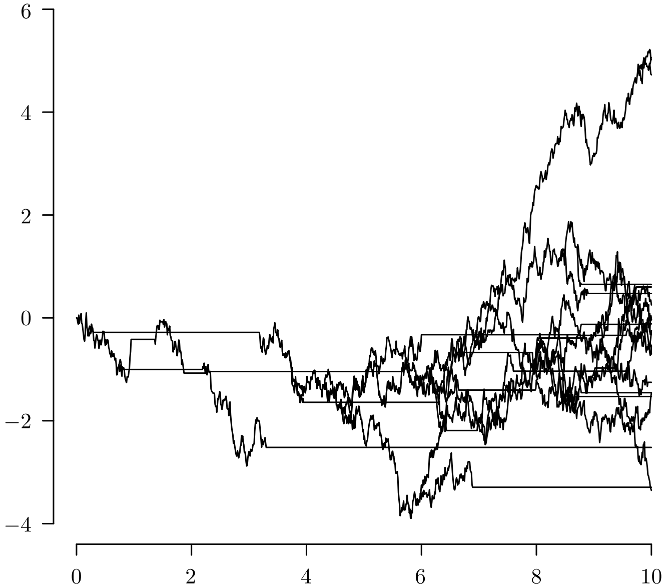


Fig. 8 A simulation of ooBBM of variant I with parameters $s = c = c' = 0.5$

Definition 3.3 (on/off BBM variant I, seed bank model) The on/off branching Brownian motion corresponding to the system (3.4) is the unique Markov process $(M_t)_{t \geq 0}$ with state space Γ evolving according to the following rules:

- Active particles (with flag $\boldsymbol{a}$) move in $\mathbb{R}$ as independent Brownian motions.
- Each active particle branches at rate s into two active particles.
- Dormant particles (with flag $\boldsymbol{d}$) neither move nor branch.
- Each active particle turns dormant at rate c, changing its flag from $\boldsymbol{a}$ to $\boldsymbol{d}$.
- Each dormant particle turns active at rate c', changing its flag from $\boldsymbol{d}$ to $\boldsymbol{a}$.

All these transitions happen independently of each other and independently for different particles. See Fig. 8 for a simulation.

Given our prior knowledge about the duality of the transformed F-KPP equation with branching Brownian motion, it is now not surprising that this process turns out to be the dual to the solution of (3.4): The dispersal term given by the Laplacian just reproduces in the dual, giving rise to the underlying Brownian motions. The switching mechanism between active and dormant translates to the backward process like in the non-spatial model in Sect. 2.2. The branching mechanism is a direct consequence of the form of the selection term given by $su(1-u)$. Since duality is a recurrent theme in this review, we provide the basic heuristic argument here: Recall the generator calculation in the proof of Theorem 2.2 and observe that the term corresponding to the selection in the generator of the Markov process corresponding to (3.4) applied to monomials u^n (as for the moment duality) is given by

$$su(u-1)\frac{\partial}{\partial u}u^n = sn\big(u^{n+1} - u^n\big).$$

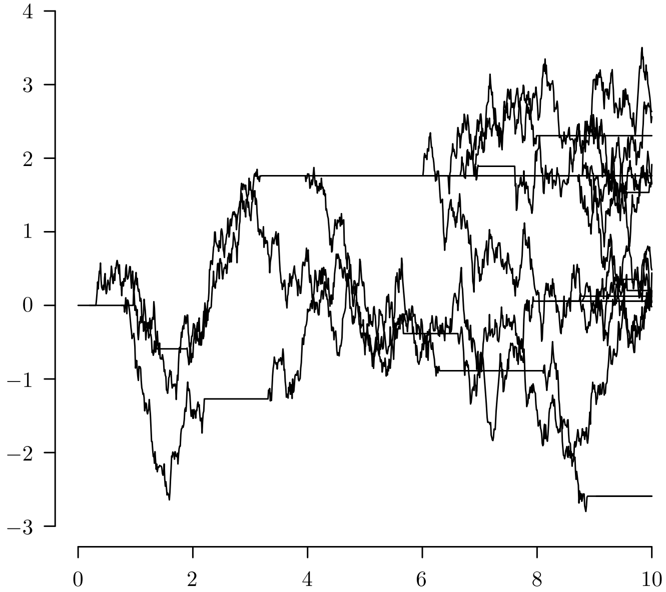


Fig. 9 A simulation of ooBBM of variant II with parameters $s = \tilde{c} = \tilde{c}' = 0.5$

Now the right-hand side is precisely the term appearing in the generator of a branching process where each particle splits into two independently at rate s (increasing the number of particles from n to $n + 1$). Hence arguments similar to those of Sect. 2.2.3 apply, though this time in a spatial setup.

The form of the second variant of our on/off BBM – corresponding to the spore model – is now not very surprising:

Definition 3.4 (on/off BBM variant II, spore model) The on/off branching Brownian motion corresponding to the system (3.5) is the unique Markov process $(\tilde{M}_t)_{t \geq 0}$ evolving according to the following rules:

- Active particles (with flag $\boldsymbol{a}$) do *not* move but independently branch at rate s each into two active particles.
- Dormant particles (flag $\boldsymbol{d}$) move in $\mathbb{R}$ as independent Brownian motions.
- Dormant particles do *not* reproduce.
- Each active particle turns dormant at rate $\tilde{c}$, changing its flag from $\boldsymbol{a}$ to $\boldsymbol{d}$.
- Each dormant particle turns active at rate $\tilde{c}'$, changing its flag from $\boldsymbol{d}$ to $\boldsymbol{a}$.

Again, all transitions happen independently of each other and independent for different particles. See Fig. 9 for a simulation.

In order to formally state the duality result we require some additional notation for on/off BBMs. Denote by N_t the total number of particles alive in an on/off BBM of variant I at time t. Label the particles at any time t by some index set of cardinality N_t. Denote by I_t the index set of the active particles at time t, and by J_t the index set of the dormant particles at time t. Then, for each particle alive at time t, labelled by some $\gamma \in I_t \cup J_t$, we denote its trajectory process in $\mathbb{R}$ by $(M_t^\gamma)_{t\geq 0}$. For variant II, we correspondingly use the notation $\tilde{I}_t$, $\tilde{J}_t$ and $(\tilde{M}_t^\gamma)_{t\geq 0}$. For example, if for $t \geq 0$ we have

$$M_t = \big((M_t^1, \boldsymbol{a}), (M_t^2, \boldsymbol{d}), (M_t^3, \boldsymbol{a}), (M_t^4, \boldsymbol{d})\big) \in \big(\mathbb{R} \times \{\boldsymbol{a}, \boldsymbol{d}\}\big)^4 \subset \Gamma,$$

then $I_t = \{1, 3\}$, $J_t = \{2, 4\}$, and $N_t = 4$.

We are now ready to formally state the spatial duality for both models. Observe that this duality is semi-probabilistic in the sense that the processes $u(t, y)$ and $v(t, x)$ appearing on the left-hand side of the duality equations are deterministic.

Proposition 3.1 (Proposition 1.8 in [14]) *Let* (u, v) *and* $(\tilde{u}, \tilde{v})$ *be the solutions to Equation* (3.4) *and* (3.5) *with initial conditions* $u_0, v_0 \in \mathcal{B}(\mathbb{R}, [0, 1])$ *and* $\tilde{u}_0, \tilde{v}_0 \in \mathcal{B}(\mathbb{R}, [0, 1])$, *respectively. Further, let* $(M_t)_{t\geq 0}$ *and* $(\tilde{M}_t)_{t\geq 0}$ *on/off BBMs of variant I and variant II, respectively, with the same parameters. Then, for variant I it holds that*

$$u(t, x) = \mathbb{E}_{(u_0,v_0)}\Big[u(t, x)^1 v(t, x)^0\Big] = \mathbb{E}_{(x,\boldsymbol{a})}\Bigg[\prod_{\alpha\in I_t} u_0\big(M_t^\alpha\big) \prod_{\beta\in J_t} v_0\big(M_t^\beta\big)\Bigg],$$

$$v(t, x) = \mathbb{E}_{(u_0,v_0)}\Big[u(t, x)^0 v(t, x)^1\Big] = \mathbb{E}_{(x,\boldsymbol{d})}\Bigg[\prod_{\alpha\in I_t} u_0\big(M_t^\alpha\big) \prod_{\beta\in J_t} v_0\big(M_t^\beta\big)\Bigg],$$

and similarly for variant II with u, v, M *replaced by* $\tilde{u}$, $\tilde{v}$, $\tilde{M}$.

With the help of these dual processes, a probabilistic representation of the solution to the Cauchy problems can be given as follows. Indeed, starting in a Heaviside initial condition, we obtain the (analogue of the classical) *McKean representation* for the solution u:

Lemma 3.1 *Let* $(R_t)_{t\geq 0}$ *be the position of the rightmost particle of an on/off branching Brownian motion of variant I started at* $M_0 = (0, \boldsymbol{a})$. *Then the solution to* (3.4) *started at* $u_0(x) := v_0(x) := \mathbb{1}_{[0,\infty)}$ *is given by*

$$u(t, x) = \mathbb{P}_{(0,\boldsymbol{a})}\big[R_t \leq x\big], \quad t \geq 0, x \in \mathbb{R}.$$

The analogous result holds for variant II.

Proof This is again a direct application of duality:

$$u(t, x) = \mathbb{E}_{u_0}\big[u(t, M_0)\big] = \mathbb{E}_x\Bigg[\prod_{\beta\in I_t} u\big(0, M_t^\beta\big)\Bigg] = \mathbb{E}_x\Bigg[\prod_{\beta\in I_t} \mathbb{1}_{[0,\infty)}\big(M_t^\beta\big)\Bigg]$$

$$= \mathbb{P}_x\Big[\min_{\beta\in I_t} M_t^\beta \geq 0\Big] = \mathbb{P}_0\Big[\max_{\beta\in I_t} M_t^\beta \leq x\Big] = \mathbb{P}_{(0,\boldsymbol{a})}\big[R_t \leq x\big],$$

for any $t \geq 0$ and $x \in \mathbb{R}$. □

A question that can thus be approached via duality for both the classical F-KPP equation as well as our two new model variants is that of the value of the critical wave-speed when started in Heaviside initial conditions. Thanks to the probabilistic representation, this directly translates into the asymptotic speed of the rightmost particle in the corresponding dual on/off Branching Brownian motion.

Theorem 3.5 (Theorem 1.10 and Proposition 1.17 in [14]) *For both variants of ooBBM, the critical wave speed exists and agrees with the asymptotic speed*

$$\lim_{t\to\infty} \frac{R_t}{t},$$

where $(R_t)_{t\geq 0}$ *is the position of the rightmost particle as in Lemma 3.1. Moreover, denoting* λ^I *resp.* λ^{II} *this limit in variant I resp. variant II, we have*

$$\lambda^{II} < \lambda^I < \lambda^*,$$

where $\lambda^* = \sqrt{2}$ *is the critical wave speed of the classical F-KPP model, cf.* (3.2).

This can be shown via martingale convergence arguments (see [14, 22]), and explicit values for given model parameters can be provided.

Biologically speaking, for each population model this wave speed corresponds to the *speed of invasion of a beneficial allele*, that is, to the speed at which an advantageous genetic variant takes over in an existing population in which both variants were originally separated. Intuitively, given common biological understanding of dormancy, seed banks should increase resilience of systems, i.e. in our case slow down the speed of invasion. Indeed, this is true for both systems, and can be explicitly quantified. Interestingly, the dormancy mechanism in variant II (spore model) seems to be significantly more efficient in slowing down invasions that the dormancy strategy of variant I (seed bank model), in particular for large selection strength s, see Fig. 10.

The systems exhibit further interesting (in particular, non-monotone) behaviour in the model parameters, which seems to be hard to interpret analytically, but where the dual process can provide valuable intuition. See the discussion section of [14], where also several open research problems are proposed.

4 Dormancy and Random Environments

So far, we have investigated the effects of different dormancy mechanisms, in particular spontaneous and responsive switching, on coalescent structures in population genetics (Sect. 2), as well as the interplay of spontaneous switching, spatial dispersal, and directional selection (Sect. 3). However, we have not yet paid attention to the question as to why a certain dormancy strategy might emerge at all, and in particular which dormancy strategy might be most effective in a given type of random environmental fluctuations, especially if dormancy comes with additional costs.

To do this, we follow [12] and consider a minimal *two-type branching process model* that incorporates active and dormant types, and evolves in a *randomly fluctuating environment*. The environment is assumed to realise only two different states

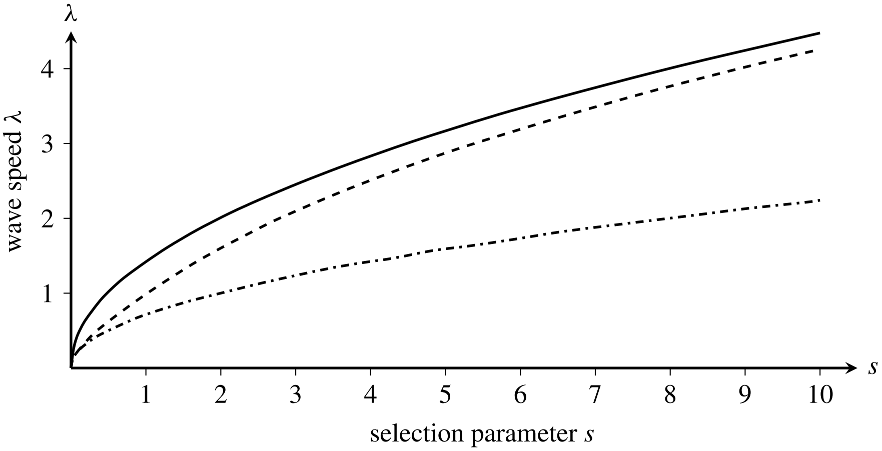
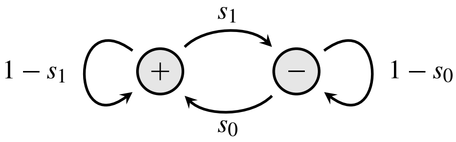


Fig. 10 Comparison of the "effectiveness" of the two dormancy strategies: In the spore model, the effect of dormancy on the wave speed is much more drastic than in the seed bank model, in particular for large s. Black line: Critical wave speed of the classical F-KPP model depending on the selection parameter s, dashed line: Variant I, dash-dotted line: Variant II

Fig. 11 Representation of the random environment with transition probabilities between the two states "+" and "–"



$\{+, -\}$, where the state "+" denotes a *healthy*, and state "−" a *harsh* environment, and evolves according to a discrete-time Markov chain whose transition probabilities are depicted in Fig. 11.

Our goal is to incorporate and investigate the following two basic dynamics in the branching process model:

- In the *stochastic switching (bet-hedging) regime*, while the overall expected reproductive output may depend on the environment and should be smaller (sub-critical) during harsh times than during (super-critical) healthy times, the proportion with which active and dormant types are produced, as well as the wake-up probabilities of the dormant type, should be independent of the state of the environment.
- In the *responsive switching regime*, the overall expected offspring numbers may again depend (in a similar fashion as above) on the state of the environment, but additionally, the reproductive policy should be affected: For example, the production of dormant types should be favoured during harsh times (and wake-up probabilities should be reduced), whereas during healthy times, more active types should be produced (and wake-up probabilities should be increased).

Moreover, both of the above strategies should have a lower expected total offspring number than a corresponding branching process without dormant types, in order to reflect the costs of being capable to engage in dormancy.

We now turn these ideas into a concrete bi-type Bienaymé-Galton-Watson (BGW) process in random environment.

Definition 4.1 (Environmental process) Let $E = (E_n)_{n\geq 0}$ be the discrete time $\{+, -\}$-valued Markov chain with transition probabilities $s_1 \in (0, 1]$ (from $+$ to $-$) and $s_0 \in (0, 1]$ (from $-$ to $+$) as depicted in Fig. 11. This chain will be called the *environmental state process*. We further assume stationarity, i.e. that E_0 starts in its unique stationary distribution.

Definition 4.2 (BGW process with dormancy in random environment) We define a two-type BGW process conditional on the environment E as follows:

- **Active offspring:** Let $(\xi^+_{n,i})_{n\in\mathbb{N},i\in\mathbb{N}}$ and $(\xi^-_{n,i})_{n\in\mathbb{N},i\in\mathbb{N}}$ be two independent families of pairs of independent and identically distributed discrete random variables, with distributions

$$\xi^\pm_{1,1} = ((\xi^\pm_{1,1})_1, (\xi^\pm_{1,1})_2) \sim \mu^\pm \in \mathcal{M}_1(\mathbb{N}_0 \times \mathbb{N}_0).$$

  Here, the superscripts "+" resp. "−" refer to the state of the environment, n should be considered a generation, and i the index of an individual within this generation. The two components 1 and 2 of $\xi^\pm_{n,i}$ correspond to active and dormant offspring numbers, respectively. For example, $\xi^+_{n,i}$ denotes the number of active and dormant offspring of an (active) individual i in generation n within a healthy environment. We denote the corresponding expected values by

$$m^\pm_j := \mathbb{E}\big[(\xi^\pm_{1,1})_j\big] \quad \text{for} \quad j \in \{1, 2\},$$

  and the variances by $\sigma^2_\pm := \mathbb{V}\big[(\xi^\pm_{1,1})_1 + (\xi^\pm_{1,1})_2\big] < \infty$.
- **Dormant offspring:** Let $(\zeta^\pm_{n,i})_{n\in\mathbb{N},i\in\mathbb{N}}$ denote a family of iid discrete random variables on $\{0, 1\}^2$ with distribution given by

$$\mathbb{P}\big[\zeta^\pm_{1,1} = (0,0)\big] = d^\pm \in [0, 1 - w^\pm], \qquad \mathbb{P}\big[\zeta^\pm_{1,1} = (1,0)\big] = w^\pm \in [0, 1],$$
$$\mathbb{P}\big[\zeta^\pm_{1,1} = (0,1)\big] = 1 - d^\pm - w^\pm, \qquad \mathbb{P}\big[\zeta^\pm_{1,1} = (1,1)\big] = 0.$$

  These random variables describe the resuscitation (via creation of one active individual, with probability $w^\pm$), death (with probability $d^\pm$), and persistence (with probability $1 - d^\pm - w^\pm$) of the dormant individuals in the process, again for each given environmental state.

Then, the process $(Z_n)_{n\geq 0}$ on $\mathbb{N}_0 \times \mathbb{N}_0$ with $Z_0 = (1, 0)$ and

$$Z_{n+1} := \mathbb{1}_{\{E_{n+1}=\text{“}+\text{”}\}} \cdot \left(\sum_{i=1}^{(Z_n)_1} \xi^+_{n,i} + \sum_{i=1}^{(Z_n)_2} \zeta^+_{n,i}\right) + \mathbb{1}_{\{E_{n+1}=\text{“}-\text{”}\}} \cdot \left(\sum_{i=1}^{(Z_n)_1} \xi^-_{n,i} + \sum_{i=1}^{(Z_n)_2} \zeta^-_{n,i}\right)$$

for $n \geq 0$ is called a *BGW process with dormancy in environment* $E = (E_n)_{n\geq 0}$.

With these specifications, we can investigate the effects of the environment for the long term growth and survival of our branching process with dormancy. Note that while the offspring law of the dormant individuals is explicitly given, for the active individuals, we will only be concerned with the expected offspring numbers that we collect together in a mean matrix. More precisely, for each environmental state, we consider the conditional offspring mean matrices:

$$M^+ = \begin{pmatrix} m_1^+ & m_2^+ \\ w^+ & 1 - w^+ - d^+ \end{pmatrix}, \qquad M^- = \begin{pmatrix} m_1^- & m_2^- \\ w^- & 1 - w^- - d^- \end{pmatrix},$$

and require that $m_1^+ + m_2^+ > 1$ in the healthy environmental state, and $m_1^- + m_2^- < 1$ in the harsh state.

To model responsive and stochastic switching strategies as outlined above, we may for example choose in the *responsive regime*

$$M^+ := \begin{pmatrix} m^+ & 0 \\ w & 0 \end{pmatrix}, \qquad M^- := \begin{pmatrix} 0 & m^- \\ 0 & 1 - d \end{pmatrix}.$$

In this somewhat extreme example, if the environment is in the healthy state, the process produces only active offspring, and in the harsh state, produces only dormant types.

In the *stochastic regime*, in each environmental state, both active and dormant offspring can be produced, and their relative sizes should be independent of the environmental state. One way to realise this could be as follows: Let $\alpha \in (0, 1)$, $m_1, m_2, w > 0$ and consider the conditional mean matrices

$$M^+ := \begin{pmatrix} m_1 & m_2 \\ w & 1 - w - d \end{pmatrix}, \qquad M^- := \begin{pmatrix} \alpha m_1 & \alpha m_2 \\ w & 1 - w - d \end{pmatrix}.$$

Here, the expected proportions of active and dormant offspring stay the same, even if the overall expected offspring number of the active individuals is reduced by a fraction of α during the harsh times. Wake-up and death probabilities are completely independent of the environmental state.

To describe the long-term behaviour of our two-type branching process Z in environment E, we consider its *Lyapunov exponent*, which can be defined in the stationary and ergodic random environmental case as follows: Let

$$\begin{aligned} \varphi_Z &:= \lim_{n\to\infty} \frac{1}{n} \log \mathbb{E}\big[(Z_n)_1 + (Z_n)_2 \mid (E_k)_{1\le k\le n}\big] \\ &= \lim_{n\to\infty} \frac{1}{n} \log \Big\| (1, 0) \cdot \prod_{k=1}^{n} (M^+)^{\mathbb{1}_{\{E_k=\text{``}+\text{''}\}}} \cdot (M^-)^{\mathbb{1}_{\{E_k=\text{``}-\text{''}\}}} \Big\|_1 . \end{aligned}$$

General theory tells us that this limit exists and is deterministic, and that long-term survival, i.e. $\mathbb{P}\big[Z_n \to 0\big] < 1$, is possible if and only if $\varphi_Z > 0$, see e.g. [42]. Note that in the case of survival, a positive Lyapunov exponent can be interpreted as the exponential growth rate of the underlying population, i.e. as a Malthusian parameter.

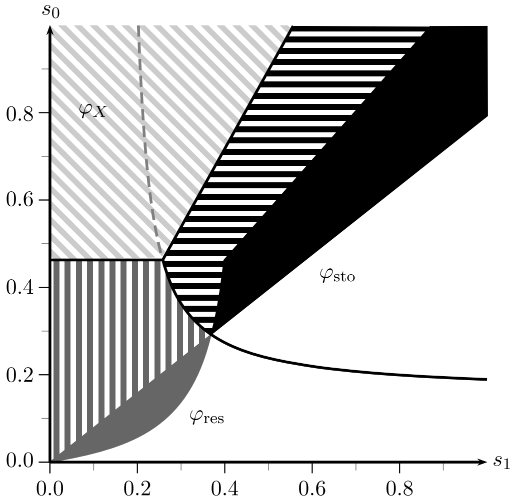


Fig. 12 Optimality of switching strategies. The solid-filled areas indicate where a certain strategy is optimal in the sense that it is the only strategy with a positive Lyapunov exponent. In the shaded regions, the corresponding strategy is still optimal, but not the only strategy with a positive Lyapunov exponent, allowing long- term survival. The dark-grey regions correspond to the responsive switching regime, the black regions to the stochastic switching regime, and the light-grey region to a branching process without dormancy trait (but higher expected offspring number). Details can be found in [12].

Unfortunately, it is in general a notoriously hard problem to evaluate the asymptotics of the random matrix product appearing in φ_Z explicitly. However, for the mean matrices in the above two special set-ups, the Lyapunov exponent can be computed rather easily, at least for some parameter choices: In the responsive case, both mean matrices are of rank 1, while in the stochastic case, we can exploit that $\det M^- = \alpha \det M^+$ and

$$(M^+)^{\mathbb{1}_{\{E_k=\text{“+”}\}}}(M^-)^{\mathbb{1}_{\{E_k=\text{“–”}\}}} = \begin{pmatrix} \alpha^{\mathbb{1}_{\{E_k=\text{“–”}\}}} m_1 \\ w \end{pmatrix} \cdot (1, \tfrac{m_2}{m_1}) + \begin{pmatrix} 0 \\ 1 \end{pmatrix} \cdot (0, \tfrac{\det M^+}{m_1}),$$

which in combination with the additional assumption that the parameters ensure that $\det M^+ = 0$, yields explicit results. Details of the analysis are carried out in [12].

We refrain from giving the concrete formulas for φ_Z (which can be found in [12]), but instead provide a general picture in Fig. 12. The rough take-home message is the following:

- Stochastic switching / bet hedging is often optimal in environments that change frequently and ‘unpredictably’.
- Responsive switching is often optimal if changes are less frequent, and in particular when harsh times are really bad.
- If the impact of the environment is not very severe, then developing a costly dormancy trait may not be necessary.

The details of course depend on the specific of the strategies and the involved parameters. Related results for phenotypic switching can be found in [28], see also [51, 59].

5 Further Work on Dormancy, and Areas for Future Research

The theory of dormancy in interacting (in particular, biological) systems is currently quite quickly expanding, opening up several roads for research in both theoretical and applied scenarios. Therefore, we conclude this article by highlighting further developments and briefly indicate areas for potential future mathematical research.

The dormancy processes from Sect. 2.2 where studied in more detail e.g. in [8], where the boundary behaviour of the seed bank diffusion is studied through polynomial diffusions. The seed bank coalescent was also intensively studied with regards to its shape [36], its use for statistical tools for seed bank detection in [9] and extended to other reproductive mechanisms in [37]. The duality relation was strengthened by the derivation of the important *look down construction* for the seed bank in [32].

One area that is rapidly expanding is that of *spatially structured models in population biology*. The interplay of dispersal and dormancy, and its consequences for genetic-, species-, and community diversity, is an active area in ecology (see e.g. Wisnoski et al. [70]). On the mathematical side, Greven, den Hollander and Oomen [38–40], introduced a seed bank model on *discrete (infinite) geographic space*, where each colony has its own local seed bank. A crucial innovation in this model is that these local seed banks can also be structured into (countably many) layers. These *layered seed banks* then allow for *heavy-tailed wake-up times*, leading to new universal scaling behaviour. In particular, the classical *"coexistence vs. clustering dichotomy"* is shifted towards coexistence by *deep* seed banks, thus supporting the maintenance of diversity.

Further recent work in this direction includes spatially inhomogeneous populations with seed banks, cf. [25, 26, 61], and models involving even a continuum of seed banks (an idea suggested by Dario Spanò), see [49, 50], leading to new (continuum) multi-type coalescents. The interplay of the resulting heavy-tailed wake-up times in other spatial systems, e.g. the F-KPP setup from the previous section, is largely open, posing challenging future research questions.

In general, models with very old – or very deep – seed banks, such as [5, 6, 11, 44], can lead to somewhat degenerate coalescents, or non-Markovian ancestral renewal structures. It would in particular be interesting to discuss in how far such models can give rise to a "fractional Wright-Fisher diffusion".

Regarding *stochastic adaptive dynamics* (see e.g. [21, 34]), where populations move in a *trait space* and undergo birth, death, competition and mutation in a measure-valued process set-up, dormancy has been considered as an evolutionary force only very recently. Here, it has been shown that dormancy traits can establish themselves despite additional reproductive costs if they in turn provide a higher tolerance for competitive pressure [3], and may lead to new coexistence regimes in the presence of horizontal gene transfer in models for bacterial populations [4, 17]. Beyond maintaining diversity, it has been shown that dormancy may even generate diversity by enabling *speciation*, see [18] for a result in the sympatric speciation scenario of Dieckmann and Doebeli [27]. A systematic analysis of its interplay with the different scaling regimes for mutation rates, as well as for complex fitness landscapes is again an area for future research.

Scenarios for *population dynamics in random environments* (or fluctuating selection) pose many technical challenges, and beyond the above-mentioned works [28] and [12] there seem to be few rigorous probabilistic works in truly random environments (but see [65]). This seems to be an important gap in the present probabilistic theory, since dormancy often has evolved as a specific response to unpredictable environments. Future research is this direction, also incorporating spacial models or complex trait spaces, will be required to get a grasp for the large variety of dormancy mechanisms.

For seasonal environments, recent work by [23] shows that dormancy can lead to non-classical genealogies, and even speciation may be caused by such temporally fluctuating selection [24]. Note that this speciation mechanism is different from the one mentioned above in [18], since the former rests on seasonal environments, while the latter is a result of the interplay of competitive pressure and a certain (static) fitness landscape.

Many diseases, in particular persistent infections and cancer (on the individual level), or virus epidemics (on the population level) involve dormancy phenomena in one form or the other (e.g. [15]). For example, in cancer, therapy failure due to short-term dormancy, or relapses due to long-term metastatic latency, pose difficult problems in current oncology (see e.g. [16, 35] and the references therein). Here, future research will likely be highly interdisciplinary, and opens up many perspectives for population dynamic modelling, simulation and analysis with dormancy.

In the above list, we have mainly focused on research motivated from biology / the life sciences. But there are also interesting developments in the area of statistical physics, where dormancy, or more generally, switching phenomena, on the micro-level can lead to novel behaviour (such as uphill-diffusion) on the macro area, see e.g. [33]. Also, dormancy and switching can be incorporated in classical systems of interacting particles, such as the contact process [15, 56], or models from evolutionary game theory [64].

The topic will likely keep mathematicians (in particular probabilists) busy for some years to come.

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